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Compensatory growth in crossbred Aberdeen Angus and Belgian Blue steers: Effects on the colour, shear force and sensory characteristics of *longissimus* muscle

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Abstract

The effect of feed restriction (99 days) followed by compensatory growth during a 200 day re-alimentation period on the colour and sensory characteristics of meat from Aberdeen Angus × Holstein-Friesian (AN) and Belgian Blue × Holstein-Friesian (BB) steers was examined. Compensatory growth had no effect on muscle pH and temperature decline, chemical composition, drip loss, fat colour, or juiciness, but increased ($p = 0.009$) Warner-Bratzler shear force and decreased tenderness ($P = 0.08$) and overall flavour ($P = 0.03$). Compared to meat from BB steers, meat from AN steers had a higher intramuscular fat concentration and was rated similarly for tenderness, but higher for many of the flavour characteristics examined. While adjustment for intramuscular fat concentration removed some of these differences, genotype-specific flavour differences remained. It is concluded that genotype had greater effects of meat quality that the compensatory growth feeding regime imposed in this study.

Keywords: meat quality, compensatory growth, sensory analysis.

1. Introduction

Compensatory growth is the ability of an animal to undergo accelerated growth when offered feed ad libitum after a period of restricted feed intake (Hornick et al., 2000). In grass-based beef production systems, compensatory growth allows the realignment of feed demand from a time when feed is expensive (eg winter) to a time when feed is plentiful and cheap (spring/summer). As a result, there is a reduction in the cost of feeding the animal which can contribute to an increase in the profitability of the

production system. The literature suggests that compensatory growth is enhanced when the restriction period is relatively short (approximately 3 months) and not too severe (Hornick et al., 2000). There is considerable, but often conflicting, information on the effect of compensatory growth, and its underlying basis, on bovine meat quality, particularly its effect on meat tenderness (Sinclair et al., 2001; Hansen et al., 2006; Moloney et al., 2008). Moreover, research relating to the relative effect of compensatory growth on meat quality from breeds of differing maturity reared under a similar production system is limited. The different responses to compensatory growth across the studies cited above seem to reflect, at least in part, intramuscular fat concentration. We hypothesised that since early maturing breeds deposit more fat than late maturing breeds at a similar age, compensatory growth would have less of an impact on early maturing breeds.

Therefore, the objective of this study was to examine the effect of compensatory growth on sensory characteristics of *M. longissimus thoracis et lumborum* (LTL) muscle from Aberdeen Angus × Holstein Friesian (AN) and Belgian Blue × Holstein Friesian (BB) steers, representative of early and late maturing genotypes, respectively.

2. Materials and methods

All animal procedures were conducted under experimental licence from the Irish Department of Health and Children, in accordance with the Cruelty to Animals Act, 1876 and the European Communities Regulation 2002 and 2005. In addition, ethical approval was granted from the Animal Research Ethics Committee, University

College Dublin, Belfield, Dublin, Ireland. Animals were slaughtered in an EU-licensed abattoir, Meadow Meats Rathdowney, Co. Laois, Ireland.

2.1 Animal model and management

Sourcing and rearing of the animals used in the present study were described by Keady et al. (2011). In brief, male Spring-born progeny (n = 46) of Holstein-Friesian dams and sired by either Aberdeen Angus or Belgian Blue bulls were identified and sourced from Irish commercial herds in Autumn 2009. There was no over dominance of any particular sire within genotypes. The calves were castrated using the burdizzo method (Pang et al., 2009) within 1 mo of arrival. They were offered grass silage (228g dry matter (DM)/kg, 112 g crude protein (CP), 80 g ash, 557 g neutral detergent fibre (NDF), 351 g acid detergent fibre (ADF)/kg DM, DM digestibility 677 g/kg, pH 3.6) *ad libitum* plus 1 kg of concentrates (825 g DM/kg, 121 g CP, 43 g ash, 557 g NDF, 352 g ADF/kg DM) per head per day before commencing the study to allow adjustment to their new environment and recovery from castration. Mean age at the commencement of the study was 362 (SD. 15.5) and 369 (SD 19.4) days for AN and BB steers, respectively. Mean body weights were 295 (SD 30.0) and 287 (SD 48.6) kg for AN and BB, respectively. Within genotype, animals were blocked by weight and randomly assigned to 1 of 2 treatment groups in a 2 (genotypes) x 2 (feeding treatments) factorial design. One group (11 AN and 12 BB) was offered a high energy control diet consisting of the above concentrates *ad libitum* and 10 kg of grass silage per head daily (H-H) throughout the study. The second group (11 AN and 12 BB) was offered an energy restricted diet consisting of grass silage *ad libitum* plus 0.5 kg of concentrate per head per day for 99 days followed by *ad libitum* access to the high energy diet (H-H) until slaughter. The initial 99 days was considered the differential

feeding period. The subsequent re-alimentation period lasted 200 days with all animals slaughtered on day 299 of the study.

The animals were weighed at the start of the study (day 0), the end of the differential feeding period (day 99) and on 2 consecutive days before slaughter (day 299). Animals were also weighed every 2 to 3 weeks at the same time each morning before fresh feed was offered. On the morning of slaughter the steers were transported 130 km to The Meadow Meats commercial slaughter facility in Rathdowney, Co. Laois, Ireland. Animals were slaughtered (Halal ritual procedure) within one hour of arrival. Carcasses were hung by the Achilles tendon and moved to a chill room with an average ambient temperature of 3 °C, within one hour of slaughter. Approximately 6 hours post-mortem, the chill was set to °C.

2.2. Carcass temperature and pH post mortem

Starting at 1.5 hours *post mortem*, the temperature of the LTL muscle was recorded by making a scalpel incision between the 10^{th} and 11^{th} rib and inserting a temperature probe (Knick Portamess 913 thermometer, GmbH & Co., Berlin, Germany). The pH of the LTL was measured by insertion of a glass electrode attached to a portable pH meter (Knick Portamess 913 pH meter, GmbH & Co., Berlin, Germany), close to the insertion point of the temperature probe. The pH reading was automatically adjusted for carcass temperature. Temperature and pH were measured periodically for 8 hours post mortem and at 48 hours *post mortem.*

2.3 Collection of LTL samples

124 The right side of each carcass was cold-boned at 24 h *post mortem*. Three steaks were
125 cut from the LTL each 2.5 cm in thickness, 30cm distal to the 10^{th} rib. The adhering
126 fat was removed from the steaks and subsequently used for fat colour analysis as
127 described below. The first steak was immediately used for drip loss assessment while
128 the second steak was used for muscle colour assessment. Following this the steak was
129 vacuum packed, aged for 14 days at 4 °C, frozen at -20 °C and subsequently used for
130 Warner-Bratzler shear force (WBSF) assessment. The third steak was vacuum packed,
131 frozen at -20 °C and subsequently chemically analysed as described below. The
132 remaining LTL with subcutaneous fat intact was vacuum packed immediately, aged
133 for 14 days, frozen at - 20 °C and forwarded to the Division of Farm Animal Science,
134 University of Bristol for sensory analysis.
135
136 *2.4 Chemical composition of LTL*
137 Intramuscular fat and moisture concentrations were determined from thawed LTL
138 using the Smart System 5 microwave moisture drying oven and NMR Smart Trac
139 Rapid Fat analyser (CEM Corporation, USA) using AOAC Official Methods 985.14
140 and 985.26 (1990). Protein concentration was determined using a LECO FP328
141 (LECO Corp., MI, USA) protein analyser based on the Dumas method and according
142 to AOAC Official Method 992.15 (1990).
143
144 *2.5 Muscle drip loss*
145 Drip loss was measured using the hanging bag method (Honikel, 1998). In brief,
146 samples of LTL of a standard size (4 cm × 4 cm × 2 cm) and weight (100 g) were cut
147 and weighed at 48 hours post slaughter. Samples were suspended in plastic bags at 4

°C and were reweighed after 72 hours hanging. Drip loss was calculated as the percentage of weight lost over the 72 hour period.

2.6 Muscle and fat colour

A freshly cut sample of LTL (25 mm) was trimmed of adhering adipose tissue at 48 hours *post mortem*, wrapped with oxygen-permeable PVC film and permitted to bloom in darkness at 4°C, for 4 hours to permit oxygenation of myoglobin. Readings of '*L*' (lightness), '*a*' (redness) and '*b*' (yellowness) values were measured and muscle hue angle ('*H*') and saturation ('*C*') were calculated as $\tan^{-1}$ (*b/a*) and $[(a)^2 + (b)^2]^{0.5}$, respectively on both the muscle and the trimmed adipose tissue using a Hunterlab UltraScan XE colorimeter (Hunter Associates Laboratory, Inc., Reston, VA, USA). Final conversion of hue angle from radians to degrees was achieved by multiplying $\tan^{-1}$ (b/a) by 180/π (Liu et al., 1996). The instrument was calibrated prior to measurements using its standard white calibration tile. Four readings were made on non-overlapping areas of each sample using the optical port (Ø2.54cm) and average values were reported as final readings. Diffuse illumination (D_{65}, 10°) with an 8° viewing angle was used. The spectrocolorimeter was used in reflectance mode and the specular component was excluded.

2.7 Warner-Bratzler shear force and cooking loss

Warner-Bratzler shear force was measured according to the procedure of Shackelford et al. (1994). In brief, steaks were trimmed of external fat, weighed and cooked in open vacuum pack bags in a circulating water bath (Grant instruments Ltd., UK) set at 72 °C, until their internal temperature reached 70 °C (assessed using a Minitherm H18751 temperature probe, Hanna Instruments Ltd., UK). Steaks were cooled to room

temperature, reweighed for determination of cooking loss and tempered at 4 °C overnight. Cooking loss was determined as the difference between the weight of the steak after cooking and its initial weight prior to cooking, expressed as a percentage. Seven cores (1.25 cm diameter) parallel to the direction of the muscle fibres were collected for each steak and each core was sheared using an Instron Universal testing machine (Model no. 5543, Instron Europe, High Wycombe, Bucks, UK) equipped with a Warner Bratzler shearing device. The crosshead speed was 5 cm/min. The highest and lowest shear force measurements were excluded in the calculation of mean values. For analysis of the data, Instron Series IX Automated Materials Testing System software for Windows (Instron Corporation, Bucks, UK) was employed.

2.8 Sensory and flavour analysis

On the day before sensory assessment, samples were thawed and steaks, 1.9 cm thick, were prepared. Steaks were cooked under a conventional grill, turning every 3 minutes until the internal temperature of the muscle reached 74^{o}C as measured by a thermocouple probe. Samples, approximately 2 cm x 2 cm x 1.9 cm were then cut from the approximate centre of the steaks, avoiding areas of connective tissue, and served hot to the 10 member trained sensory panel. Each booth contained a computer screen and optical mouse as part of the computerised sensory system (Fizz, Version 2.10, Biosystems, France) for direct entry of sensory responses. See Table 1 for list of sensory and flavour terms assessed and a brief description of each.

2.9 Statistical analysis

Data were checked for normality using the UNIVARIATE procedure of statistical analysis software (SAS Institute, 2008). Ratings for livery, bitter, and rancid were

transformed by raising to the power of -0.25, 0.25 and -0.25, respectively (TransReg procedure, SAS, 2008). Data were analysed using mixed model methodology in PROC MIXED (SAS, 2008). Genotype, feeding treatment (H-H or L-H) and their interaction were included as fixed effects and sire of the animal was included as a random effect in the statistical model. For sensory data, "assessor" was also included. Where no significant interactions were observed, the data were reanalysed for main effects only. The Tukey critical difference test was performed to determine the existence of statistical differences between treatment means. For data with repeated measures (pH and temperature of carcasses at slaughter), measurement time was included as a repeated effect with an unstructured or compound symmetry covariance structure assumed among records within animal as appropriate. The choice of residual covariance structure was based on the magnitude of the Akaike Information Criterion (lowest is better). Data relating to the sensory and flavour characteristics were also analysed using intramuscular fat concentration as a co-variate. Additionally, Spearman correlation coefficients amongst meat quality values and production traits were determined using the CORR procedure of SAS.

3. Results

Unless otherwise stated, there was no significant interaction between feeding treatment and genotype for the variables examined.

3.1 Live weight and live weight gain (Table 2)

Results relating to live weight and live weight gain are described in detail in Keady et al. (2011). In brief, H-H steers were heavier than L-H steers at the end of the differential feeding period (d 99; $P < 0.001$) and this difference remained at slaughter

223 (d 299; P = 0.04) (Table 2). During the differential feeding period, H-H steers grew
224 faster (P < 0.05) than L-H steers. Compensatory growth was evident during the re-
225 alimentation period when live weight gain for H-H was lower (P < 0.05) than for L-H
226 steers.
227
228 Live weight was not affected by genotype at any stage during the study; however,
229 between d 131 and d 195 of the study, BB steers had greater (P <0.001 live weight
230 gain compared to AN steers.
231
232 *3.2 Carcass characteristics (Table 2)*
233 The carcasses from L-H steers were lighter (P = 0.003) compared to those from H-H
234 steers. There was no difference for carcass conformation while carcasses from L-H
235 steers tended (P = 0.08) to have less fat cover than those from H-H steers.
236
237 Carcasses from BB steers were heavier (P = 0.02), with superior carcass conformation
238 scores (P = <.0001) and a lower fat cover (P = <.0001) compared to those from AA
239 steers.
240 There was no effect of feeding treatment or genotype on any of the fat colour
241 variables.
242
243 *3.3 pH and temperature of LTL post mortem*
244 There was no effect of feeding treatment (P = 0.40) or genotype (P = 0.20) on LTL
245 pH and no time by feeding treatment or genotype-related interactions.
246

247 Temperature of LTL from H-H steers was higher (p=0.01) than that from L-H steers
248 but there was no effect of genotype (P = 0.46) or no time by feeding treatment or
249 genotype interactions. The pH/temperature profiles are shown together in Figure 1.
250 All carcasses passed through pH 6.0 between 35 and 15 ^{0}C. Data were not collected at
251 4.5 and 6 hours *post mortem* due to instrument malfunction.
252
253 *3.4 Chemical composition of LTL (Table 3)*
254 There was no effect of feeding treatment on the chemical composition of the LTL.
255 The concentration of protein and moisture was greater (P = 0.04) and the
256 concentration of fat was lower (<0.0001) in LTL from BB steers compared to AN
257 steers.
258
259 *3.5 Muscle drip and cooking loss (Table 3)*
260 There was no effect of feeding treatment on drip loss but drip loss was greater (P =
261 0.0043) for LTL from BB steers compared to AN steers. Cooking loss percentage was
262 greater (P = 0.03) in LTL from L-H animals compared to H-H animals, but was
263 unaffected by genotype.
264
265 *3.6 Muscle colour and pH (Table 3)*
266 Both *a* (P = 0.02) and chroma (P = 0.03) values were lower for LTL from L-H steers
267 compared to LTL from H-H steers. Lightness (P = 0.0001), *b* (P = 0.01) and hue (P <
268 0.0001) values were lower and the *a* value was higher (P = 0.01) for LTL from AN
269 steers compared to BB steers. There was no effect of feeding treatment or genotype on
270 the pH of LTL measured at 48h *post mortem*.
271

3.7 Warner Bratzler shear force (Table 3)

The LTL from L-H steers had higher (P = 0.009) WBSF values compared to LTL from H-H steers. The LTL from BB steers had higher (P = 0.04) WBSF values compared to LTL from AN steers. When adjusted for differences in intramuscular fat concentration, there was no difference between breeds but the higher WBSF values for the LTL from L-H steers remained.

3.8 Sensory and flavour characteristics of LTL (Table 4)

Scores for ease of cutting (P = 0.03), swallow (P = 0.04) and overall flavour (P = 0.03) were higher for LTL from H-H steers compared to LTL from L-H steers.

Scores for juiciness (P = 0.02), beef (P < 0.001), flavour liking (P = 0.0001), overall liking (P < 0.002), juiciness on biting (P = 0.0003), moisture (P = 0.001), pulpy (P = 0.0015), greasiness on eating (P = 0.0065), greasy residue (P = 0.0061), swallow (P = 0.02), mouth feel (P = 0.0003), pulpy residue (P = 0.0006), greasy flavour (P < 0.0001), sweet (P = 0.001), dairy (P < 0.001) and overall flavour (P = 0.0001) were higher for LTL from AN steers compared to LTL from BB steers. Scores for abnormal (P = 0.005), toughness on biting (P = 0.04), toughness on eating (P = 0.04), particles (P = 0.02), bitter (P = 0.007), acidic (P < 0.0001), cardboard (P = 0.0007) and vegetable (P = 0.01) were higher in LTL from BB steers compared to LTL from AN steers.

Data relating to the sensory and flavour characteristics were also analysed using intramuscular fat concentration as a covariate (Table 5). In this analysis, the score for overall flavour (P = 0.008) was greater in LTL from AN steers compared to LTL from BB steers. Scores for beef (P = 0.03), flavour liking (P = 0.03), overall liking (P =

297 0.002), mouth feel (P = 0.09) and dairy (P = 0.02) were higher while scores for
298 abnormal (P = 0.06) and acidic (P = 0.03) lower in AN compared to BB.
299
300 *3.9 Correlation analysis*
301 The relationships between meat quality characteristics and production variables are
302 summarised in Table 6. In summary, carcass weight was not associated with any meat
303 quality trait with the exception of cook loss for which a negative correlation was
304 observed (r = -0.33; $P < 0.05$). Similarly, growth rate prior to slaughter (day 253 -299)
305 was not correlated with the selected meat quality characteristics. There was a negative
306 correlation between WBSF and intramuscular fat (r = -0.41; $P < 0.01$) and between
307 WBSF and sensory tenderness (r = -0.45; $P < 0.01$). Intramuscular fat was negatively
308 correlated with drip loss percentage (r = -0.58; $P <0.001$) and positively correlated
309 with sensory tenderness (r = -0.32; $P < 0.05$). Drip loss was negatively correlated with
310 both sensory tenderness (r = -0.45; $P < 0.01$) and cook loss percentage (r = -0.43; $P <$
311 0.01). No statistically significant correlations were observed between pH measured at
312 48h *post mortem* and either production or meat quality variables.
313
314 **4.0. Discussion**
315 The hypothesis tested in this experiment was that compensatory growth would have
316 less of an impact on aspects of quality of the LTL muscle from an early maturing
317 breed, represented by AN sired steers, when compared to a late maturing breed,
318 represented by BB sired steers. The general lack of significant interactions between
319 genotype and feeding treatment do not support this hypothesis. Accordingly the
320 emphasis in the discussion is on the main effects of feeding treatment and genotype.
321

322

323 *4.1.1 Muscle pH and temperature post mortem.*

324 If the temperature of the carcass falls too quickly and glycolysis is slow, meat
325 toughening (cold shortening) occurs (for a review see Maltin et al., 2003; Warner et
326 al., 2010). Alternatively, if the temperature decline is slow, and glycolysis is fast,
327 toughening of the meat due to heat shortening can also occur. The rate of decline in
328 pH and was similar for both genotypes and feeding treatments, indicating that anti-
329 mortem glycogen stores were similar in all groups (Moloney et al., 2008). All
330 carcasses were chilled at a rate appropriate to avoid *post mortem* deterioration in meat
331 quality (MSA, 2013). Sinclair et al. (2001) and Moloney et al. (2008) reported that
332 growth rate before slaughter had no effect on the pattern of decline of pH or
333 temperature *post mortem* which supports the results of the current study. Fatter
334 carcasses often cool more slowly compared to leaner carcasses (Lochner et al., 1980).
335 This did not occur in the present study although AN carcasses were fatter, albeit
336 lighter, than BB carcasses. In contrast, Cuvelier et al. (2006a) reported greater
337 temperature loss 1 hour post mortem in AN bull carcasses compared to BB bull
338 carcasses which was suggested to reflect the higher carcass weight of the latter.
339 The pH values of LTL at 48 h *post mortem* were within the 'normal' range (Warriss,
340 2010).

341

342 *4.1.2 Chemical composition of LTL*

343 The lack of difference in intramuscular fat concentration between feeding treatments
344 supports the findings of Moloney et al. (2008) and likely reflects the duration of the
345 re-alimentation period. The higher intramuscular fat concentration in muscle from AN
346 in the present study supports the findings of other studies for the same genotypes

347 (Keane et al., 2011) and reflects the maturity of the AN breed compared to the BB
348 breed.
349
350 *4.1.3 Muscle and fat colour*
351 Muscle colour has a major influence on the decision to purchase meat (Carpenter et
352 al., 2011). Moloney et al. (2008) reported no difference in LTL colour variables
353 between steers offered different levels of feeding before slaughter which supports the
354 results from the current study for *L*, *b* and hue. However, *a* (redness) and chroma
355 values were lower for LTL from L-H steers compared to H-H steers. Hornick et al.
356 (1998) also reported that compensatory growth in BB bulls resulted in differences in
357 redness; however, this difference in redness was dependent on the length of the
358 restriction and re-alimentation periods. Lehnert et al. (2006) reported that nutritional
359 restriction in beef steers resulted in lower concentrations of type 2 (fast glycolytic)
360 myofibres and consequently higher levels of type 1 (slow oxidative) fibres in LTL.
361 However, during re-alimentation fibre concentrations returned to normal. The authors
362 suggest that under-nutrition and weight loss in the bovine results in a mechanism that
363 preserves slow-twitch fibres (Lehnert et al., 2006). Greater concentrations of slow-
364 oxidative fibres result in lower redness, suggesting that perhaps the compensatory
365 growth-based regime implemented here had permanent effects on fibre type. Further
366 investigation of this observation is required.
367
368 Double muscled animals have a greater percentage of white muscle fibres compared
369 to their conventional counterparts (West, 1974). Consequently, BB animals being
370 heterozygous for double muscling, likely have lower myoglobin levels in their muscle
371 and this may explain the higher *L* and lower *a* values for BB compared to AN steers.

372 The difference in redness between genotypes supports the findings of Keane et al.
373 (2011) and Cuvelier et al. (2006a, b). However, Campion et al. (2009) found no
374 difference in redness between AN and BB genotypes
375
376 Carotenoid consumption by cattle results in accumulation in adipose tissue and more
377 yellow colour (for review, see Dunne et al., 2009). That no difference in carcass fat
378 colour was observed between feeding treatments indicates that re-alimentation for 200
379 days, may have 'diluted' any effects on fat colour introduced during the differential
380 feeding period. However, whether carotenoids, once accumulated in adipose tissue,
381 remain indefinitely or are mobilised by the animal at a later stage warrants further
382 investigation (Dunne et al., 2009).
383
384 Dairy breeds have been reported as having more yellow subcutaneous fat than British
385 or European beef breeds with relatively little difference between beef breeds (Dunne
386 et al., 2009). The data in the current study support the latter observation.
387
388 *4.1.4 Muscle drip and cook loss*
389 Drip loss or exudate from beef is a source of economic loss to the processer and may
390 make the meat visually unattractive to the consumer. Hornick et al. (1998) reported
391 that compensatory growth prior to slaughter resulted in greater drip loss when the
392 restriction period was extended and suggested that this may be related to the lower fat
393 content of the muscle as a low fat content in meat is associated with higher water
394 content. Keane and Allen (2009) and Moloney et al. (2008) observed no effect of
395 feeding level prior to slaughter drip loss from muscle with a similar fat concentration.

In the current study the higher drip loss for BB could not be explained by pH at 48 h *post mortem*, Cuvelier et al. (2006b) suggested that BB bulls have greater drip loss from muscle due to a higher meat water content. Higher moisture content in LTL from BB compared to AN was also observed in the current study supporting this suggestion.

Within BB, L-H animals had a greater cooking loss compared to meat from the H-H animals; however, this was not observed within AN. Hornick et al. (1998) reported that BB bulls that exhibited compensatory growth had great cooking loss supporting the finding in the current study. In contrast, Moloney et al. (2008) reported no difference in cooking loss in Friesian steers suggesting that perhaps differences in cooking loss resulting from compensatory growth are genotype specific.

4.1.5 Warner Bratzler shear force and sensory tenderness

Tenderness is a key aspect of the eating quality of meat as indicated by consumer research (Becker et al., 1998: Moloney et al., 2001). Tenderness is frequently measured objectively as WBSF and/or subjectively using trained assessors. The moderate negative associations between the two measures of tenderness observed in the present study is similar to many other studies (Caine et al., 2003; Peachey et al., 2002) suggesting that WBSF may not always be a reliable indicatory of tenderness as perceived by the consumer.

The higher WBSF in LTL from the L-H steers is consistent with the trend reported by Moloney et al. (2008) of a higher WBSF in LTL form animals that exhibited compensatory growth compared to LTL from those on a continuous plane of nutrition.

The WBSF results are consistent with the sensory data in that tenderness (tendency) and ease of cutting were lower and toughness on biting was higher in meat from L-H compared to H-H steers. Sinclair et al. (2001) reported that pre-slaughter growth rate had no effect on meat tenderness; Therkildsen et al. (2008; 2011) reported that a compensatory growth feeding regime may improve tenderness in meat from Friesian bulls and cows, but this was muscle-type specific in bulls; Moloney et al. (2008) reported a tendency for a decrease in beef tenderness due to compensatory growth. The data in the present study support the latter observation. In the current study, factors that influence tenderness such as muscle composition and the pattern of pH and temperature decline (Maltin et al., 2003) were similar across feeding treatments. While growth rate close to slaughter was similar for both feeding treatments, L-H steers grew faster in the early part of the re-alimentation period. This suggests that early compensatory growth had an impact on tenderness that persisted subsequently andwarrants further investigation.

Cuvelier et al. (2006a, b) found no difference in WBSF values in meat from AN and BB bulls aged for 2 days and 8 days, respectively. In the current study, where the meat was aged for 14 days, the greater WBSF values observed in LTL from BB compared to AN animals was supported by the sensory tenderness. That this difference between genotypes was removed when the data were adjusted for differences in intramuscular fat concentration highlights the interaction between tenderness and fatness in muscle and the difficulty in comparing genotypes *per se*. Similarly, when Homer at al. (1997) adjusted sensory data for a range of breeds, to the average fatness of each breed, there was no difference in tenderness between steaks from ANand BB sired cattle. More directly, Chambaz et al. (2003) compared the

446 sensory characteristics of muscle from AN, Charolais and Limousin steers slaughtered
447 at a common intra-muscular fat concentration and found no difference between
448 genotypes (muscle form Simmental steers was rated more tender than AN and
449 Limousin).
450
451 It should be noted that though differences were observed between feeding treatments
452 for WBSF, even the higher average value of 33 N recorded for the L-H would be
453 considered tender (Huffmann et al., 1996).
454
455 *4.1.6 Sensory flavour analysis*
456 Hocquette et al. (2010) reported that intramuscular fat concentration directly affected
457 juiciness and flavour of beef but that tenderness was influenced indirectly. As the
458 difference in intra-muscular fat concentration due to feeding treatment was small, the
459 minor effects on flavour characteristics were not unexpected. A difference of 2 units
460 on an 8 point scale for overall liking is unlikely to be detected by an untrained
461 consumer.
462
463 Sinclair et al. (2001) reported that juiciness, flavour and overall acceptability were
464 greater in LTL from AN compared to Charolais steers. However, when sensory
465 analysis was carried out on *M. biceps femoris* from the same animals there was no
466 difference in juiciness or beef flavour between the genotypes. The higher juiciness of
467 LTL from AN in the present study most likely reflects the greater intramuscular fat
468 concentration since, when the data were adjusted differences in juiciness and most of
469 the other "flavours" disappeared. This observation is in agreement with Hornick et al.
470 (2000) and Sinclair et al. (2001). Similarly, Homer et al. (1997) found no differences

across breeds for juiciness, beef flavour and abnormal flavour. Chambaz et al. (2003) observed no difference between the breeds examined for flavour intensity and preference.While flavour liking and overall liking, which is arguably a better indication of consumer satisfaction, remained higher for AN when adjusted for intramuscular fat concentration in the present study, the magnitude of the difference is unlikely to be detected by an untrained consumer.

5.0 Conclusion

Under the conditions of this experiment, nutritional restriction followed by compensatory growth during a 200 day re-alimentation period had no lasting effects, either positive or negative, on most of the meat quality characteristics measured. However, this feeding regime increased WBSF and tended to decrease overall liking but it is unlikely that these effects would be detected by an untrained consumer.

Compared to meat from BB steers, meat from AN steers was rated similarly for tenderness, but higher for many of the flavour characteristics examined. While adjustment for intramuscular fat concentration removed some of these differences, small genotype-specific flavour differences remained. The lack of interaction between genotype and feeding treatments leads us to reject our main hypothesis and it is concluded that genotype has a greater effect of meat quality than compensatory growth.

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Table 1
Definition of terms used for sensory analysis of beef samples

Term	Definition
Tenderness	Texture of the sample for tough to tender
Juiciness	Juiciness of the sample from dry to juicy
Beef	Amount of cooked beef flavour
Abnormal	Amount of abnormal beef flavour
On cutting	
Ease of cutting	Ease with which sample is cut through by knife
Cleanness of cut	Appearance of sample on cutting with knife (jagged fibres to very clean cutting)
Initial eating	
Toughness	Amount of resistance to teeth on initial chewing
Juiciness	Amount of moisture in the sample on initial chewing
Sponginess	Amount of springiness in the sample, bounce back to bite
Crunchy	Amount of perceived crispness in the sample on initial chewing
On eating	
Toughness	Toughness on eating
Moisture	The perceived moisture content in the sample during eating
Pulpy	Pulpiness in the sample on eating
Chewiness	The total perceived effort required to prepare the sample to a state ready for swallowing
Gristle	Amount of gristle in the sample
Fibres	Amount of perceived fibres in the sample on eating
Greasiness	Amount of perceived oil or fatty matter in the sample on eating
Dissoluble	Degree to which it melts or disintegrates in mouth
Residue	
Greasy	Amount of greasy coating in the mouth
Swallow	Degree to which the residue is easy to swallow
Particles	Fine particles in residue
Pulpy	Pulpiness in the residue
Mouthfeel	Sensation in the mouth after chewing (dry or wet)
Flavour	
Greasy	The taste associated with fresh oil and fat.
Bloody	The taste associated with raw undercooked meat
Livery	The taste associated with liver flavour
Metallic	Tangy metal taste
Bitter	The taste on the tongue associated with caffeine/quinine
Sweet	The taste on the tongue associated with sugars
Rancid	The taste associated with rancid oil and fat.
Fishy	The taste associated with fish.
Acidic	The taste associated with acids
Cardboard	The taste associated with smell of damp cardboard
Vegetable	Flavour of green vegetables and grass
Dairy	The taste associated with milk products

Table 2
Effect of genotype and feeding treatment on live animal and carcass characteristics of Aberdeen Angus (AN) and Belgian Blue (BB) sired steers.

Variable	Genotype (G)			Feeding treatment[1] (F)			P-value	
	AN	BB	SED	H-H	L-H	SED	G	F
Live weight, kg								
Start, d 0	307	288	7.010	296	298	6.894	0.79	1.00
End of differential feeding period, d 99	404	390	14.124	438	356	6.894	0.99	<.0001
Realimentation, d 132	452	438	13.616	474	416	6.894	0.99	<.0001
Slaughter, d 299	655	644	10.914	669	630	6.989	1.00	0.04
Live weight gain, kg/d								
Differential feeding period, d 0 to 99	1.06	1.12	0.052	1.55	0.63	0.050	0.28	<.0001
Realimentation period, d 99 to 131	1.50	1.50	0.097	1.26	1.74	0.093	0.98	<.0001
Realimentation period, d 131 to 195	1.65	1.90	0.07	1.63	1.91	0.06	0.0007	0.0001
Realimentation period, d 195 to 253	1.34	1.33	0.09	1.34	1.33	0.09	0.89	0.87
Realimentation period, d 253 to 299	0.91	0.64	0.18	0.84	0.71	0.17	0.14	0.47
Entire period, d 0 to 299	1.25	1.26	0.038	1.33	1.18	0.036	0.81	0.0004
Carcass weight	354	369	5.860	373	350	5.538	0.02	0.0003
Carcass conformation	7.25	9.08	0.411	8.33	8.02	0.402	<.0001	0.44
Fat class	10.39	7.96	0.478	9.59	8.75	0.466	<.0001	0.08
Fat colour								
L (lightness)	68.07	67.65	0.815	67.84	67.87	0.794	0.61	0.97
a	7.73	7.35	0.658	7.75	7.34	0.640	0.57	0.52
b	14.82	15.37	0.346	15.14	15.06	0.336	0.12	0.81
Hue[2]	62.77	64.75	1.626	63.14	64.39	1.585	0.23	0.44
Chroma[3]	16.66	17.02	0.566	16.96	16.72	0.546	0.53	0.66

[1]H-H = *ad libitum* access to feed throughout the study; L-H = Restricted feeding for 99 days followed by *ad libitum* access to feed until slaughter. Production data from Keady (2011)
[2]Hue = $[\tan^{-1} (b/a)] \times [180/\Pi]$.
[3]Chroma = saturation/colour intensity = $\sqrt{(a^2 + b^2)}$.

Table 3
Effect of genotype and feeding treatment on characteristics of the *longissimus thoracis et lumborum* muscle from Aberdeen Angus (AN) and Belgian Blue (BB) sired steers.

Variable	Genotype (G)			Feeding treatment[1] (F)			P-value	
	AN	BB	SED	H-H	L-H	SED	G	F
Composition								
Protein, %	21.69	22.41	0.327	21.87	22.24	0.318	0.04	0.25
Moisture, %	70.35	73.37	0.684	71.67	72.04	0.665	0.0001	0.58
Fat, %	7.45	3.64	0.787	5.90	5.18	0.767	<.0001	0.35
Ash, %	1.09	1.11	0.030	1.08	1.12	0.030	0.77	0.27
Drip loss, %	1.41	2.07	0.209	1.67	1.81	0.200	0.004	0.48
pH (48h)	5.53	5.54	0.040	5.53	5.54	0.039	0.66	0.65
Muscle colour								
L (lightness)	35.18	37.37	0.491	36.30	36.25	0.479	0.0001	0.90
a	15.09	14.19	0.329	15.04	14.24	0.321	0.01	0.02
B	8.51	9.01	0.197	8.91	8.61	0.192	0.02	0.13
Hue[2]	29.62	32.60	0.471	30.84	31.38	0.448	<.0001	0.24
Chroma[3]	17.50	16.94	0.358	17.63	16.82	0.348	0.13	0.03
WBSF[4], N	25.29	32.63	2.801	25.09	32.83	2.731	0.014	0.009
WBSF[5], N	27.94	30.59	3.629	25.80	32.70	2.651	0.471	0.016
Cooking loss[6], %	28.71	28.37	0.572	27.89	29.19	0.559	0.56	0.03

[1]H-H = *ad libitum* access to feed throughout the study; L-H = Restricted feeding for 99 days followed by *ad libitum* access to feed until slaughter.
[2]Hue = $[\tan^{-1} (b/a)] \times [180/\Pi]$.
[3]Chroma = saturation/colour intensity = $\sqrt{(a^2 + b^2)}$.
[4]Warner-Bratzler shear force.
[5]Warner-Bratzler shear force adjusted using intramuscular fat concentration as a covariate
[6]Genotype × feeding treatment interaction (P = 0.03).Values equal 28.70, 28.72, 27.07, 29.67 for AN/H-H, AN/L-H, BB/H-H, BB/L-H, respectively.

Table 4
Effect of genotype and feeding treatment on the sensory characteristics of *M. longissimus thoracis et lumborum* muscle from Aberdeen Angus (AN) and Belgian Blue (BB) sired steers

Trait	Genotype (G)			Feeding treatment[1] (F)			P-value	
	AN	BB	SED	H-H	L-H	SED	G	F
Attributes[2]								
Tenderness	4.58	4.21	0.231	4.60	4.19	0.225	0.12	0.08
Juiciness	5.23	4.95	0.109	5.12	5.06	0.107	0.02	0.60
Beef	4.60	4.23	0.079	4.43	4.40	0.078	<.0001	0.72
Abnormal	2.34	2.60	0.088	2.40	2.54	0.085	0.005	0.12
Hedonic[2]								
Flavour liking	5.13	4.67	0.100	4.99	4.81	0.098	0.0001	0.07
Overall liking	4.81	4.35	0.141	4.71	4.45	0.129	0.002	0.09
Cutting[4]								
Ease of cutting	50.02	44.51	3.301	50.85	43.69	3.178	0.11	0.03
Cleanness of cut	60.69	57.27	2.398	59.05	58.05	2.328	0.16	0.43
Initial Bite[4]								
Toughness	46.48	53.89	3.338	47.34	53.03	3.231	0.04	0.09
Juiciness	55.38	49.40	1.448	52.42	52.37	1.412	0.0003	0.97
Sponginess	23.42	23.03	1.326	24.19	22.26	1.256	0.77	0.14
Crunchy	29.23	28.54	1.831	28.11	29.66	1.749	0.71	0.38
Eating[4]								
Toughness	44.32	51.50	3.315	45.20	50.63	3.231	0.04	0.10
Moisture	55.91	49.73	1.665	53.44	52.20	1.624	0.001	0.45
Pulpy	61.65	55.25	1.811	58.63	58.27	1.766	0.0015	0.84
Chewiness	42.13	48.18	3.349	42.73	47.59	3.267	0.08	0.15
Gristle	8.23	7.61	1.391	7.66	8.18	1.356	0.66	0.70
Fibres	46.38	50.19	2.021	48.56	48.01	1.970	0.07	0.78
Greasiness	18.52	14.59	1.335	16.38	16.73	1.301	0.007	0.79
Dissoluble	43.13	40.41	2.86	43.58	39.95	2.736	0.35	0.20
Residue[4]								
Greasy	20.07	15.25	1.619	17.12	18.20	1.579	0.006	0.50
Swallow	54.71	48.09	2.727	54.15	48.65	2.598	0.022	0.04
Particles	43.65	46.33	1.120	45.53	44.45	1.069	0.024	0.32
Mouth feel	59.27	52.77	1.577	55.87	56.17	1.538	0.0003	0.85
Pulpy	61.85	56.00	1.491	59.87	57.99	1.454	0.0006	0.21
Flavour[4]								
Greasy	18.00	11.31	1.349	14.51	14.81	1.315	<.0001	0.82
Bloody	5.62	5.60	0.733	5.80	5.42	0.714	0.97	0.59
Livery[3]	0.65	0.64	0.018	0.64	0.65	0.017	0.70	0.53
	(5.60)	(5.96)		(5.96)	(5.60)			
Metallic	9.22	10.77	1.033	10.42	9.57	1.007	0.15	0.40
Bitter[3]	1.40	1.52	0.043	1.43	1.49	0.042	0.007	0.17
	(3.84)	(5.34)		(4.18)	(4.92)			
Sweet	16.95	11.91	1.383	14.71	14.16	1.332	0.001	0.68
Rancid[3]	1.25	1.27	0.081	1.24	1.27	0.079	0.82	0.69
	(0.41)	(0.40)		(0.43)	(0.38)			
Fishy	2.65	2.51	0.199	2.51	2.66	0.187	0.49	0.43
Acidic	5.65	8.59	0.628	6.88	7.36	0.602	<.0001	0.43
Cardboard	13.02	17.29	1.108	14.32	15.98	1.079	0.0007	0.14
Vegetable	12.25	14.24	0.762	13.31	13.18	0.742	0.01	0.86
Dairy	24.40	16.34	1.500	21.76	18.97	1.461	<.0001	0.07

[1] H-H = *ad libitum* access to feed throughout the study; L-H = Restricted feeding for 99 days followed by *ad libitum* access to feed until slaughter.
[2]Eight point scale.
[3]Adjusted data - values in parenthesis represent back transformed means.
[4]One hundred line scale.

Table 5
Effect of genotype and feeding treatment on the sensory characteristics of *M. longissimus thoracis et lumborum* muscle from Aberdeen Angus (AN) and Belgian Blue (BB) sired steers adjusted using intramuscular fat concentration as a covariate

Trait	Genotype (G)			Feeding treatment[1] (F)			P-value	
	AN	BB	SED	H-H	L-H	SED	G	F
Attributes[3]								
Tenderness	4.46	4.31	0.313	4.57	4.19	0.228	0.63	0.12
Juiciness	5.08	5.06	0.133	5.08	5.07	0.096	0.85	0.93
Beef	4.53	4.28	0.104	4.41	4.40	0.076	0.03	0.95
Abnormal	2.35	2.59	0.121	2.41	2.54	0.088	0.06	0.14
Hedonic[3]								
Flavour liking	5.04	4.75	0.130	4.97	4.82	0.095	0.03	0.12
Overall liking	4.73	4.49	0.141	4.70	4.52	0.131	0.002	0.09
Cutting[5]								
Ease of cutting	49.79	45.84	4.474	51.19	44.45	3.275	0.39	0.05
Cleanness of cut	60.66	57.81	3.293	60.08	58.38	2.406	0.39	0.48
Initial Bite[5]								
Toughness	47.95	51.33	4.419	47.25	52.02	3.228	0.45	0.15
Juiciness	53.31	50.99	1.707	51.83	52.47	1.247	0.18	0.61
Sponginess	23.22	23.54	1.762	24.26	22.51	1.296	0.86	0.19
Crunchy	29.30	28.46	2.471	28.12	29.64	1.814	0.73	0.41
Eating[5]								
Toughness	46.61	49.63	4.417	45.81	50.43	3.227	0.49	0.16
Moisture	53.70	51.44	2.010	52.81	52.32	1.469	0.27	0.74
Pulpy	60.15	56.41	2.382	58.21	58.35	1.740	0.12	0.93
Chewiness	43.46	47.16	4.576	43.10	47.52	3.343	0.42	0.19
Gristle	8.37	7.50	1.919	7.69	8.17	1.402	0.66	0.74
Fibres	47.14	49.60	2.763	48.77	47.96	2.018	0.38	0.69
Greasiness	16.97	16.60	1.517	16.23	17.34	1.112	0.80	0.32
Dissoluble	42.33	43.00	3.739	44.05	41.27	2.738	0.85	0.31
Residue[5]								
Greasy	19.40	18.75	1.795	17.98	20.17	1.319	0.72	0.11
Swallow	53.98	50.11	3.584	54.46	49.64	2.631	0.29	0.08
Particles	43.67	46.36	1.509	45.55	44.48	1.109	0.09	0.34
Mouth feel	58.35	54.93	1.959	56.12	57.16	1.437	0.09	0.47
Pulpy	60.06	57.39	1.851	59.37	58.08	1.352	0.16	0.35
Flavour[5]								
Greasy	15.39	13.55	1.294	13.79	15.14	0.935	0.17	0.16
Bloody	5.69	5.54	1.028	5.82	5.41	0.743	0.88	0.58
Livery[4]	0.64	0.65	0.025	0.64	0.65	0.017	0.63	0.40
	(5.96)	(5.60)		(5.96)	(5.60)			
Metallic	10.19	9.93	1.356	10.68	9.44	0.980	0.85	0.22
Bitter[4]	1.44	1.49	0.056	1.45	1.49	0.040	0.40	0.31
	(4.30)	(4.93)		(4.42)	(4.93)			
Sweet	16.47	14.11	1.717	15.19	15.38	1.236	0.18	0.87
Rancid[4]	1.25	1.26	0.114	1.24	1.27	0.082	0.99	0.74
	(0.41)	(0.40)		(0.42)	(0.38)			
Fishy	2.69	2.44	0.270	2.50	2.63	0.195	0.38	0.53
Acidic	5.87	7.69	0.791	6.69	6.87	0.569	0.03	0.76
Cardboard	14.67	15.87	1.287	14.77	15.77	0.930	0.35	0.29
Vegetable	12.54	13.99	1.058	13.39	13.14	0.765	0.18	0.75
Dairy	23.61	18.78	1.848	22.16	20.23	1.332	0.02	0.16

[1] H-H = *ad libitum* access to feed throughout the study; L-H = Restricted feeding for 99 days followed by *ad libitum* access to feed until slaughter. [3] Eight point scale. [4] Adjusted data - values in parenthesis represent back transformed means. [5] One hundred point scale.

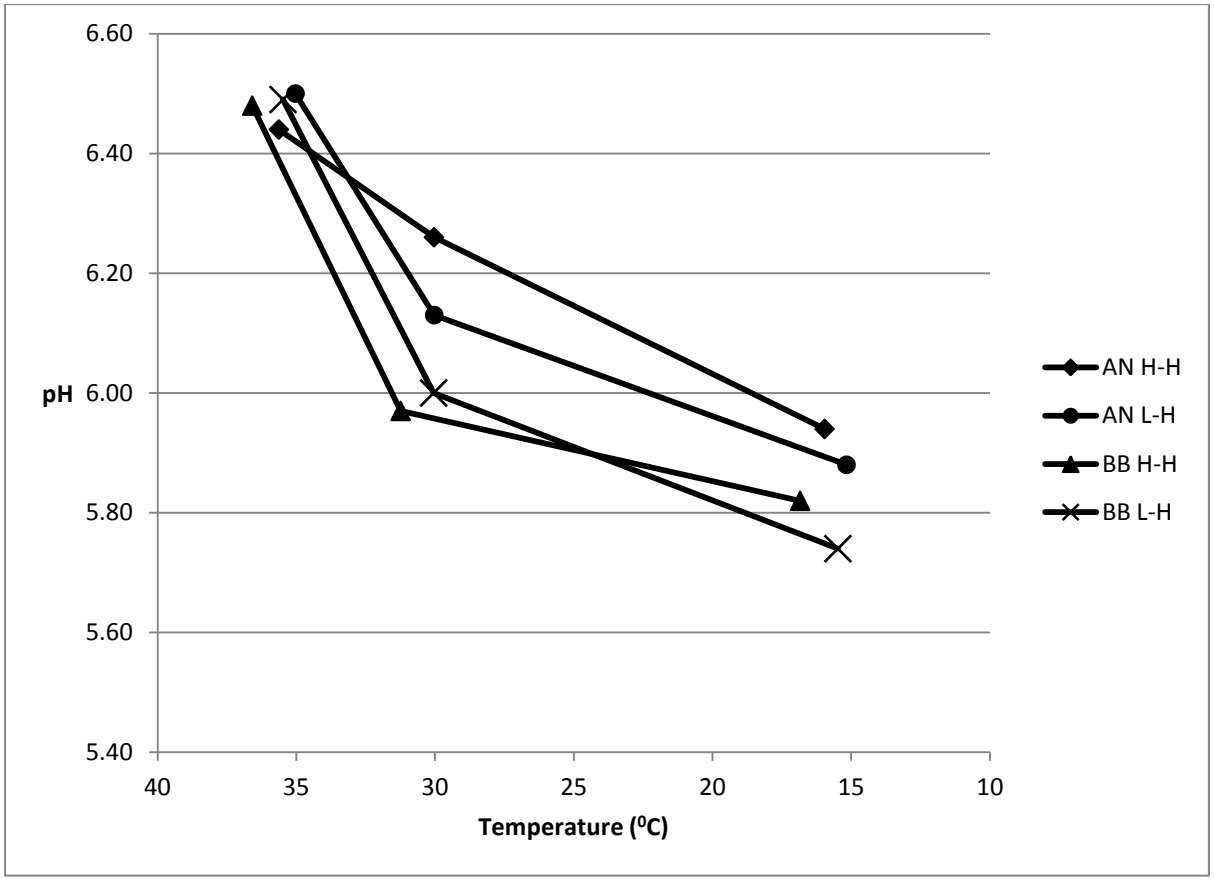
Table 6
Associations[1] between production variables and meat quality traits

Variable	CW[2]	ADG[3]	WBsf[4]	pHU[5]	IMF[6]	Drip loss	Tenderness[7]
ADG[3]	0.10						
WBsf[4]	-0.28	0.28					
pHU[5]	-0.24	0.23	0.13				
IMF[6]	-0.05	0.107	-0.41**	-0.02			
Drip loss	0.27	0.08	0.24	-0.13	-0.58***		
Tenderness[7]	-0.07	-0.11	-0.45**	-0.15	0.32*	-0.45**	
Cook loss	-0.33*	-0.23	0.18	0.006	0.007	-0.43**	0.13

[1]Values presented are Spearman correlation coefficients *r* from unadjusted data.
[2]Cold Carcass weight
[3]Average daily gain prior to slaughter (day 253-299)
[4]Warner-Bratzler shear force
[5]Ultimate pH at 48 h
[6]Intramuscular fat percentage
[7]Sensory tenderness
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Fig. 1. *Post mortem* pH and temperature decline. AN = Aberdeen Angus; BB = Belgian Blue. H-H = *ab libitum* access to feed throughout the study; L-H = Restricted feeding for 99 days followed by *ad libitum* access to feed until slaughter.

Figure


6.60
6.40
6.20
pH 6.00
5.80
5.60
5.40
40
35
30
25
20
15
10
Temperature (⁰C)
AN H-H
AN L-H
BB H-H
BB L-H